Pacific Science (1978), vol. 32, no. 1

Food Availability and Egg Production: A Field Experiment with *Hippa pacifica* Dana (Decapoda; Hippidae)[1]

CRAIG FUSARO[2]

ABSTRACT: The effect of augmented diet on egg production for *Hippa pacifica* was tested in the crab's natural habitat, the sandy beaches at Enewetak Atoll, Marshall Islands. Crabs on a treatment beach were fed cubed shark meat for 18 days. After treatment, the percentage of ovigerous female *H. pacifica* had nearly doubled, while a nearby control beach did not change significantly.

FACTORS THAT CONTROL EGG PRODUCTION for crustaceans have been the subject of much discussion. The variation in seasonality of egg production within some groups, in particular, has shown that environmental temperature alone cannot account for many egg production cycles. For example, Boolootian et al. (1959) presented data on five Pacific coast crab species inhabiting the same latitude (about 36° N), three of which exhibited annual reproductive cycles while two others did not. Turquin (1975) described distinct reproductive periodicity in cavernicolous peracaridans living in a presumably temperature- and light-constant environment. Goodbody (1965) reported that *Emerita portoricensis* bred continuously on beaches of Jamaica. Cox and Dudley (1968) suggested that for *E. analoga*, age (or size) modified the female's egg production response to environmental conditions. Wenner (1977) suggested that food availability influenced the timing of egg production for *Hippa pacifica* at Hawaii.

There is evidence that food availability affects egg production for some crustaceans under laboratory conditions. Hines (1976) found that the percentage of *Chthamalus fissus* brooding eggs increased with food dose, and Vijverberg (1976) demonstrated that both the mean number of eggs per female and the number of young produced per female per week increased as food concentration increased for *Daphnia hyalina*. Little evidence is available, however, that shows the effects of food availability on egg production for crustacean populations in nature in an experimental, rather than observational sense.

At Enewetak Atoll, Marshall Islands, an excellent opportunity for such testing is presented by populations of *Hippa pacifica* Dana, the Pacific mole crab. These anomuran crabs inhabit sandy beaches of the various islands of the atoll in abundance. They live between high- and low-tide zones, buried in the sand (Hanson 1969, Wenner 1977). Unlike their filter-feeding confamilial relative *Emerita analoga*, these crabs are opportunistic scavengers. They sit just below the sand surface with their highly setose first thoracic legs extended above the sand surface to entrap small prey items and/or catch bits of debris. Wenner (1977) reported that at Hawaii, *H. pacifica* eats *Physalia*, the Portuguese man-of-war, and at Enewetak the crabs may eat planktonic mysids washed ashore.

The crabs are recruited from a common planktonic zoeal population within the atoll lagoon to beaches of isolated islands. Once established on a particular island beach, the crabs are essentially a benthic infaunal

[1] This research was supported by a grant through the Mid-Pacific Marine Laboratory from the U.S. Energy Research and Development Administration. Manuscript received 16 November 1977.

[2] University of California, Santa Barbara, Marine Science Institute, Santa Barbara, California 93106.

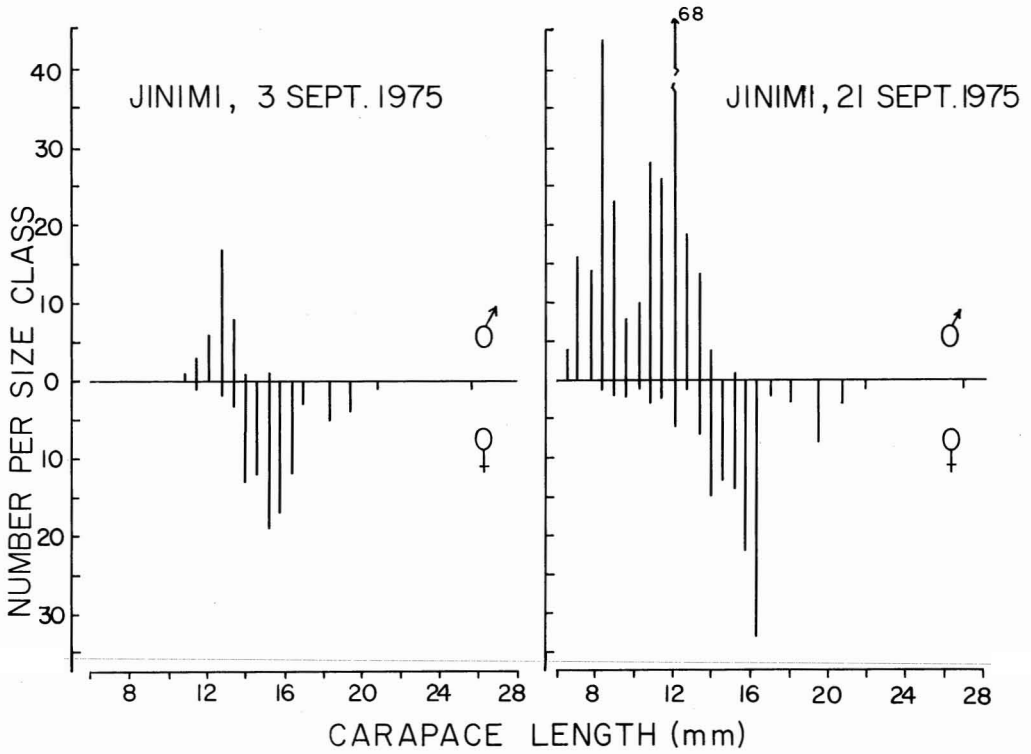

FIGURE 1. Size-frequency histogram of *Hippa pacifica* on Jinimi Island, the treatment beach, before (3 September) and after (21 September) treatment.

species, and are thereby isolated from other such island populations. All the islands of the atoll experience the same constant water temperature (29 $\pm$ 1° C), and thus temperature is eliminated as an experimental variable. A field experiment was therefore conducted at Enewetak Atoll to examine the effects of food availability on egg production by *Hippa pacifica*.

PROCEDURES

The procedure used to examine the effects of food availability on egg production for *Hippa pacifica* was simple. Two islands of the atoll were chosen for testing because they (1) exhibited similar, low percentages of ovigerous females and (2) were close enough together on the atoll to ensure similar recent environmental histories. First, each beach was sampled to determine population structure. The animals were gathered by placing a skewered piece of gray reef shark (*Carcharinas mentisorrah*) meat at the top of the wash zone of the lagoon-side sand beaches. *Hippa pacifica* could be observed moving up the beach toward the bait. After 5 min had elapsed, the sand around the bait was gathered up and sieved for crabs, which were then automatically sorted by size in a sorter fully described by Wenner et al. (1974). Data on the size-frequency structure, size-specific sex ratio, and size-specific number of ovigerous females were recorded, and the crabs were returned to the beach immediately after counting. About 32 percent of the females at Jinimi (Clyde) Island, the treatment beach, were initially ovigerous, while about 38 percent of the females at Bokandretok (Walt) Island, the control beach, were ovigerous.

Treatment consisted of feeding the mole crabs on the beach at Jinimi an unusually large amount of an acceptable food. Gray

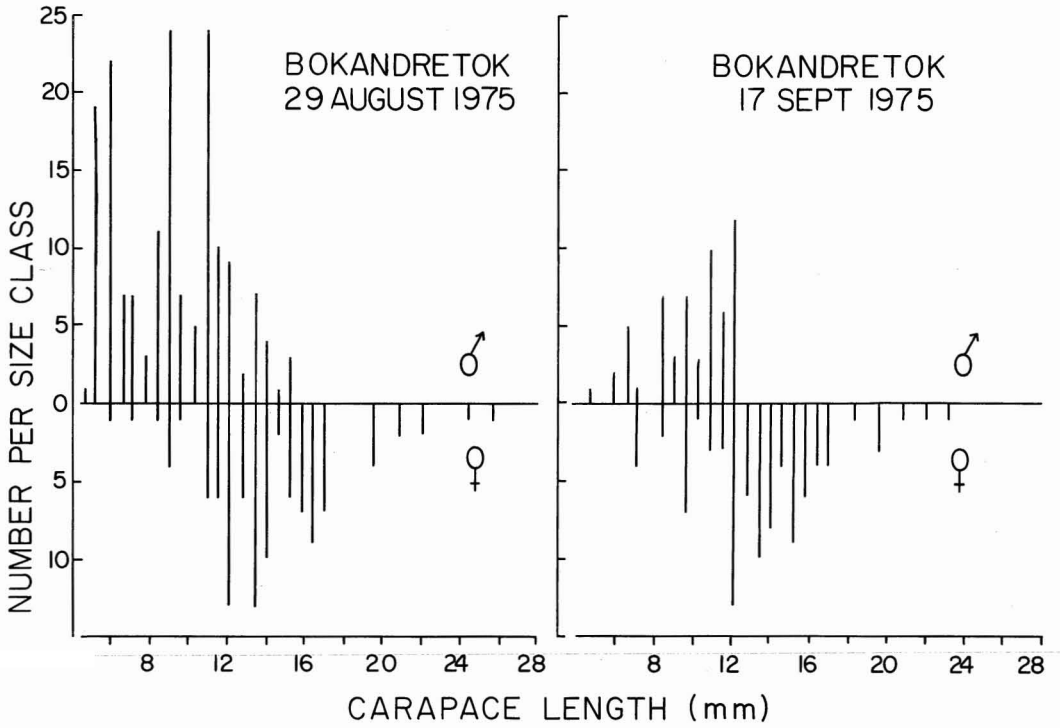

FIGURE 2. Size-frequency histogram of *Hippa pacifica* on Bokandretok Island, the control beach.

reef shark was chosen as food because (1) *Hippa pacifica* in all sizes come readily to this meat placed on the beach as bait, (2) Wenner (1977) demonstrated that shark was preferred by *H. pacifica* over many other types of foods even though shark is not apparently a part of its regular diet, and (3) shark is readily available at the atoll. The meat was cut into small cubes, about 2 cm square, and buried approximately 1 to 2 cm deep about 0.3 m apart in the wash zone, throughout the length of the treatment beach. Approximately 1.5 kg of shark meat was placed on the treatment beach each day for 18 days of treatment, or about 27 kg total. Based on an estimate of 5 to 15 crabs per meter of beach (Wenner, personal communication) on the approximately 100-m treatment beach, somewhere between 18 and 54 g of shark meat were added to the diet of each crab on the beach. Since the crabs range in weight between about $\frac{1}{2}$ to 3 g, the extra food supplied in 18 days of treatment was equivalent to several times their body weight. The crabs accepted the food as readily as they accepted shark meat placed as bait. Both beaches were sampled subsequently to monitor changes in each population.

RESULTS

Size-frequency histograms for populations of *Hippa pacifica* on Jinimi Island (the treatment beach) and Bokandretok Island (the control beach) indicate that size-frequency structure in general changed little at either beach during the 18-day treatment period (Figures 1 and 2). At Jinimi the posttreatment sample includes a mode of small crabs not apparent in the pretreatment sample (Figure 1). These small individuals, however, are below the minimum size at which *H. pacifica* carries eggs, and thus are not of consequence here. A slight increase in size was evident for females in the 15- to 16-mm mode at Jinimi,

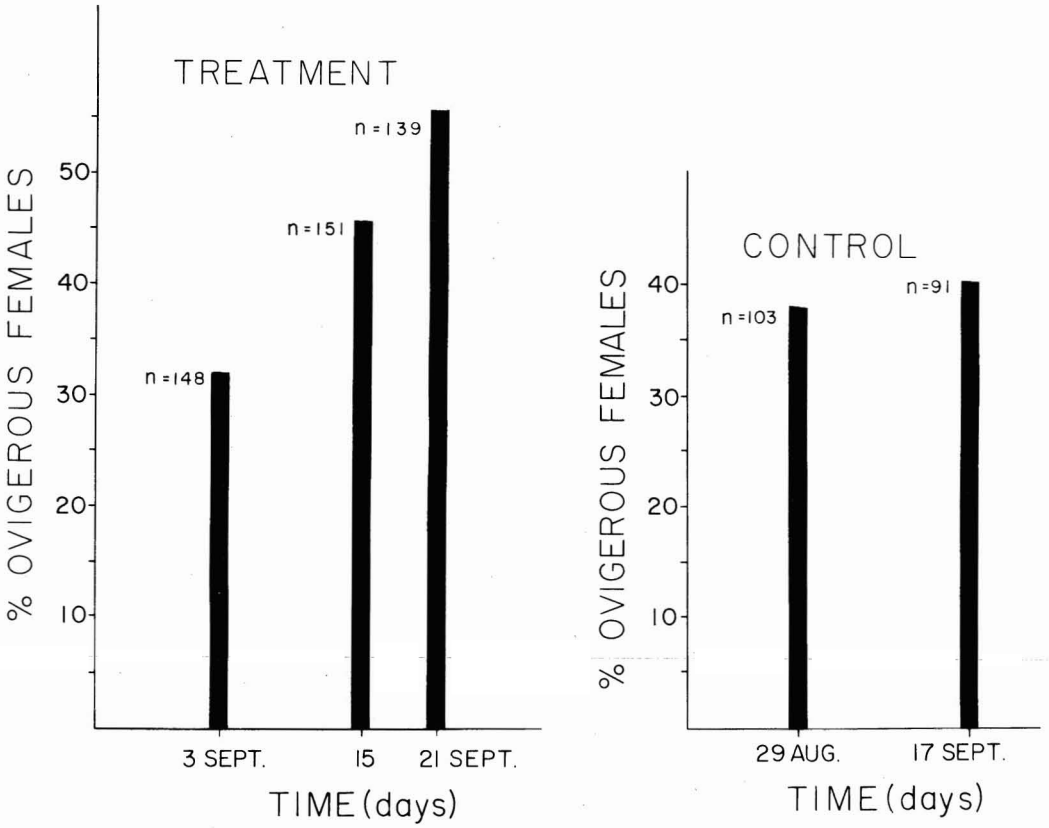

FIGURE 3. Percentage of ovigerous female *Hippa pacifica* as a function of time during the course of treatment for Jinimi (treatment) and Bokandretok (control) beaches.

but in general, the location of modes in these polymodal distributions was not much different between pre- and posttreatment samples. Thus, during the 18-day treatment period, overall size-frequency structure showed no major changes at either the treatment or the control beach with respect to modes of potentially mature female *H. pacifica*.

The difference in percentages of ovigerous females in pre- and posttreatment samples from the treatment and control beaches, however, was striking (Figure 3). No significant change ($\chi^2 = 0.281$, $0.5 < p < 0.7$) occurred on the control beach, while the percentage of ovigerous females on the treatment beach changed from 32.4 percent to 56.1 percent ($\chi^2 = 48.4$, $p < 0.001$) during the treatment period.

DISCUSSION

Data on egg production cycles for *Hippa pacifica* at Enewetak Atoll do not exist. Wenner (1977) presented egg production data for the species on the island of Oahu, Hawaii, indicating that local populations of the crab may exhibit percentages of ovigerous females approaching 100 percent. Fusaro (1975) presented the data for *H. pacifica* egg production at Enewetak Atoll that are reproduced here in Table 1. These data indicate that at Enewetak the percentage of ovigerous females could also approach 100 percent. In general, though with several exceptions, the downcurrent (western) islands tended to have a higher percentage of ovigerous females than did the upcurrent (eastern) islands (Figure 4, Table 1). One potential environmental differ-

TABLE 1

PERCENTAGE OF OVIGEROUS FEMALE *Hippa pacifica* AT VARIOUS ISLANDS OF ENEWETAK ATOLL SAMPLED DURING THE FALL IN 1973 AND 1975

ISLAND	NUMBER OF CRABS, *n*	1973	NUMBER OF CRABS, *n*	1975
Enjebi	302	16	58	79
Elle			16	100
Eleleron	361	38		
Aomon–Bijire	124	1		
Runit			100	60
Ananij	222	76	8	75
Jinimi			148	32
Jedrol			40	92
Japtan	177	31	44	91
Medren			63	92
Bokandretok			103	38
Enewetak, marine pier	149	7	304	93
Enewetak, cargo pier	435	71	30	92
Ikuren	292	73		
Mut	307	90		
Boken	197	80	134	96
Ribewon			216	89
Kidrenen			432	91
Biken	159	68		

ence between the two groups of islands may be drift food brought to downcurrent beaches and not to upcurrent beaches. Data on plankton distribution in and around the atoll (Johnson 1954) suggest that most production occurs within the lagoon, and that the surrounding ocean is relatively devoid of plankton compared to densities within. Surface water moves from east to west through the lagoon continuously (Mao and Yoshida 1955), and lagoon-produced surface plankton must be carried with it to the downstream (western) islands. If this is actually the case, the western islands would have a richer surface plankton supply, barring substantial surface eddies at the eastern edge.

The above possibilities led to the formulation of this test of the effects of food abundance on egg production to examine the possibility that an enriched food supply would produce an elevated percentage of ovigerous females. Egg number per female was not included in the test because that would have involved sacrificing the female, and sampling without replacement would have depleted the populations significantly. The results displayed in Figure 3 illustrate that the female mole crabs on Jinimi that were not carrying eggs were capable of producing eggs given the appropriate conditions —an increased food supply.

In summary, it was found that for *Hippa pacifica* at Enewetak Atoll, food availability influenced the proportion of the female population that was ovigerous. Thus, *H. pacifica* may be said to be food-limited at the atoll with respect to egg production.

ACKNOWLEDGMENTS

I wish to thank Adrian Wenner for his continued constructive criticism throughout this work. I also wish to thank J. Childress, A. Oaten, and J. King for their critical review of the manuscript.

LITERATURE CITED

BOOLOOTIAN, R. A., A. C. GIESE, A. FARMANFARMAIAN, and J. TUCKER. 1959. Reproductive cycles of five west coast crabs. Physiol. Zool. 32:213–220.

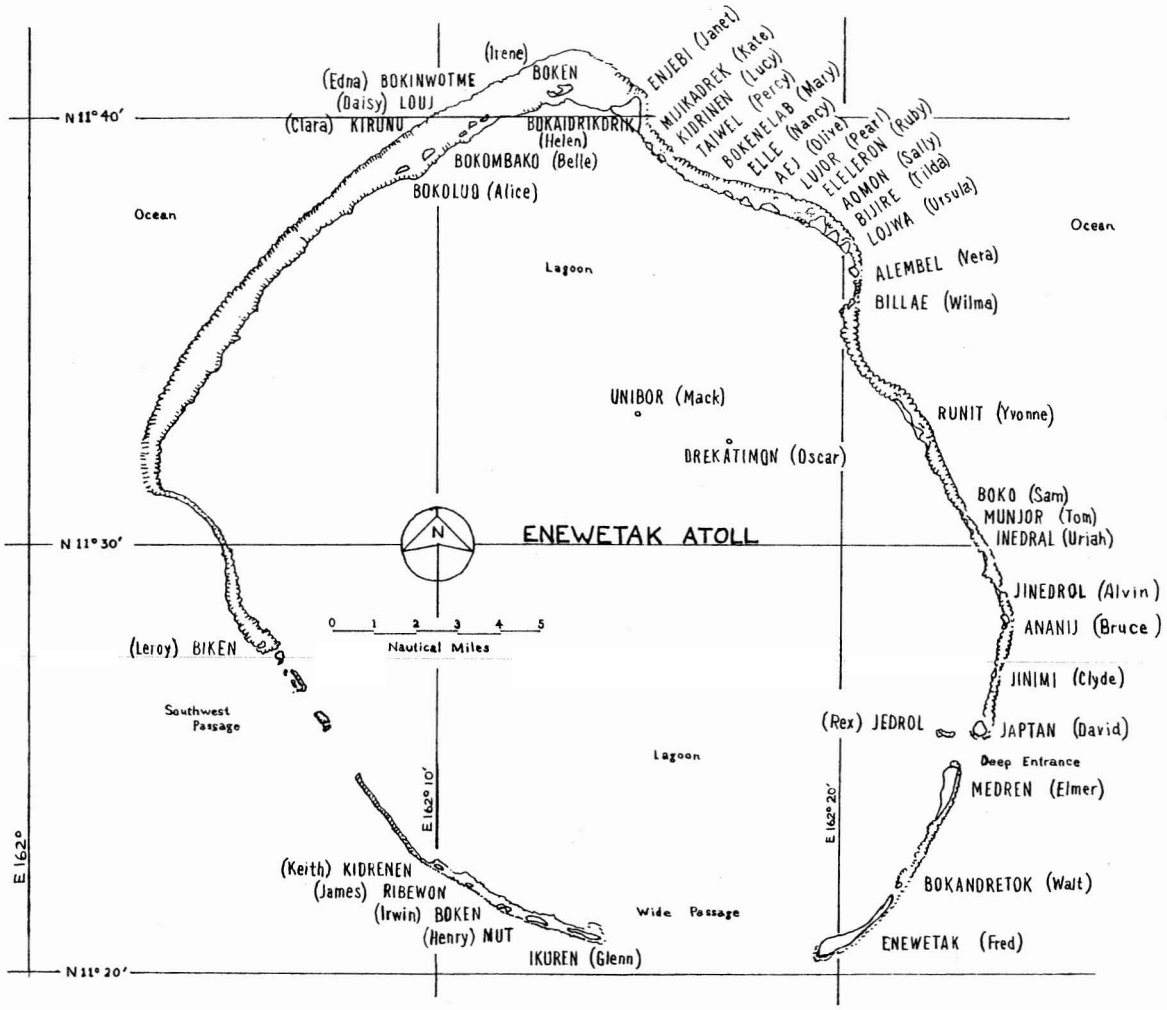

FIGURE 4. Map of Enewetak Atoll, showing relative positions of various islands mentioned in the text and Table 1. Ocean currents in this vicinity are predominantly from the east, and the tradewinds blow for most of the year from the northeast at Enewetak Atoll.

COX, G. W., and G. H. DUDLEY. 1968. Seasonal patter of reproduction of the sand crab *Emerita analoga* in Southern California. Ecology 49:746–751.

FUSARO, C. 1975. Egg production in *Hippa pacifica*: a means for detection of food distribution. Report of Research Activities, Mid-Pacific Marine Laboratory.

GOODBODY, I. 1965. Continuous breeding in populations of two tropical crustaceans, *Mysidium columbiae* (Zimmer) and *Emerita portoricensis* Schmidt. Ecology 46:195–197.

HANSON, A. J. 1969. The life history of the sand crab *Hippa cubensis* Saussure living on a small island. M.S. Thesis. University of British Columbia, Vancouver.

HINES, A. H. 1976. Comparative reproductive ecology of three species of intertidal barnacles. Ph.D. Thesis. University of California, Berkeley.

JOHNSON, M. W. 1954. Plankton of Northern

Marshall Islands. U.S. Geol. Surv., Prof. Paper 260-F:301–314.

MAO, HAN-LEE, and K. YOSHIDA. 1955. Physical oceanography in the Marshall Islands area. U.S. Geol. Surv. Prof. Paper 260-R:647–754.

TURQUIN, M. J. 1975. Cycle biologique et rhythme de ponte chez les crustacés aquatiques troglobies. C.R. Acad. Sci., Paris 280(17):2033–2036.

VIJVERBERG, J. 1976. The effect of food quantity and quality on the growth, birth rate, and longevity of *Daphnia hyalina* Leydig. Hydrobiologia 51:99–108.

WENNER, A. M. 1977. Food supply, feeding habits and egg production in Pacific mole crabs (*Hippa pacifica* Dana) Pac. Sci. 31: 39–47.

WENNER, A. M., C. FUSARO, and A. OATEN. 1974. Size at onset of sexual maturity and growth rate in crustacean populations. Can. J. Zool. 52:1095–1106.